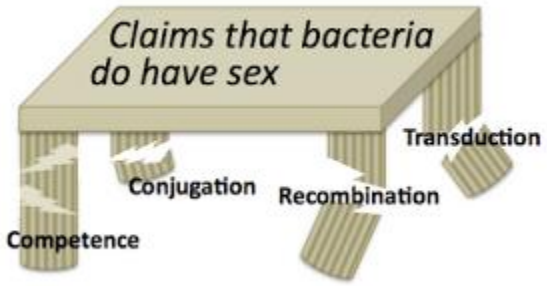
http://sandwalk.blogspot.com.br/2012/07/do-bacteria-have-sex.html?m=1

Sandwalk

Strolling with a skeptical biochemist

Thursday, July 19, 2012

Do Bacteria Have Sex?



There are three different ways for bacterial to exchange information: conjugation, transduction, and transformation. Do any of these count as sex?

It depends on your definition. Rosie Redfield and I had a discussion about this when we were together in Ottawa. I think some species of bacteria do engage in sex because all three mechanisms can result in gene exchange between different individual bacteria. I think that transformation and conjugation may have arisen, in part, as a way of repairing damaged DNA and escaping the effects of Muller's Rachet.

Rosie thinks that sex, by definition, means mixis—the shuffling of alleles due to sex as in eukaryotes. Here's how she explains it in a recent post on her blog [Claims that Bacteria Do Have Sex].

This work addresses a very important question with big/deep/fundamental importance to the colossal problem of the origin of meiotic sex in eukaryotes. The question is 'Do bacteria have any processes that evolved because of selection for recombination of chromosomal alleles?' We think this selection is the reason for the success of meiotic sexual reproduction in eukaryotes, but compelling evidence for this has been elusive. Bacteria have four well-studied processes that do generate homologous recombination; three that transfer DNA between cells and one that carries out homologous recombination. But almost every aspect of these processes has been shown to cause recombination as an unselected side effect of processes selected for other functions.

I don't think sex evolved in eukaryotes in order to promote mixis so this argument doesn't resonate with me.

Read Rosie's post if only to discover why she thinks transformation evolved. She's thinking of applying for a grant to study this problem so I'm sure she would appreciate your feedback.

[Image Credit: Rosie Redfield]

Laurence A. Moran at Thursday, July 19, 2012

Share

33 comments:

1.

Rosie Redfield Thursday, July 19, 2012 5:56:00 PM

It's not true that I think that 'sex, by definition, means mixis. Instead, I recognize that the word 'sex' has many valid meanings in different contexts. Because of this, I mostly avoid using the word sex In the context of my research.

For my research, the most useful meanings are either 'any process that evolved to randomize combinations of alleles' or 'the meiotic sexual reproduction of eukaryotes'. If I do refer to 'sex', I take pains to be sure the audience understands which meaning I intend.

Above Larry used 'sex' to mean any process that generates new combinations of alleles. With that intended meaning, he's entirely justified in concluding that bacteria do engage in sex. In general, discussions about genetic exchange in bacteria are more productive if the word sex is not used.

Reply

Replies

1.

Laurence A. Moran Friday, July 20, 2012 12:03:00 PM
Actually I don't think that sex is "any process that generates new combinations of alleles."

I think sex is any process that brings in pieces of DNA from an outside source and allows it to recombine with the native genome. I think that sex arose as a mechanism of repair, not a way of making new combinations of alleles.

Mixis is an epiphenomenon.

Reply

2.

S Johnson Thursday, July 19, 2012 6:49:00 PM

Mixis is a cellular mechanism. I would have thought that the evolution of mixis would involve the cooptation of other mechanisms that evolved for other purposes. Which is to say, these bacterial genetic exchange mechanisms are transitional to mixis. And the question would be which one(s)?

Mixis would also involve coopting structures to form the spindle etc. wouldn't it?

Reply

3.

AnonymousThursday, July 19, 2012 7:01:00 PM

How would you detect low-frequency bacterial fusion? That would count as bacterial sex.

Reply

4.

Rosie Redfield Thursday, July 19, 2012 7:39:00 PM

@S. Johnson: None of the known processes that lead to 'genetic exchange' (really one-way DNA transfer and recombination) appear to have any relationship to meiotic sexual reproduction. None of them involve anything even faintly related to cell fusion, much less meiosis.

@Anonymous: Low-frequency fusion could be detected using two strains, each carrying several selectable alleles at widely separated chromosomal locations. But unless there turned out to be an evolved mechanism to make it happen (not just rare accidents), I don't think it could be called a bacterial equivalent of sexual reproduction.

Reply

Replies

1.

AnonymousThursday, July 19, 2012 9:28:00 PM

Why would there need to be an evolved mechanism if the frequency of rare accidents was sufficient to avoid the ratchet?

Reply

5.

Allan Miller Friday, July 20, 2012 4:50:00 AM

Personally, I think equating sex with recombination is misleading. Much of the focus on finding a 'reason' for (the-kind-of-) sex (that-we-are-most-interested-in) has focussed upon the recombinational aspect, and although that has the most far-reachng consequences, it is almost incidental - a secondary feature of an ancestral process of syngamy and reduction.

That there is commonality between bacterial recombinational processes and eukaryotic ones is undeniable - after all, it boils down to basic chromosome management, which is likely to be ancient - strand damage repair and so on. But to lump the grosser consequences together is misleading - it is not necessarily the case that the reason recombination exists is the same in both cases, even though many of the pathways may be common.

Before eukaryotic homologous recombination could arise, a stable cycle of syngamy and reduction must have preceded it. It is less likely that syngamy/reduction occurred *in order to* reciprocally swap chromosome segments, for whichever of the many distant consequences of that act one favours.

I think that the explanation is more local - advantages from diploidy, or a nutritional gain for both partners. Within a syngamy/reduction cycle, homologues are paired to ensure equal partition. DSBs automatically invoke the repair pathway, and there are 4 ways of resolving the junction. 2 are recombinant, and 2 are not - and there is (AFAIK) no information available to the resolving enzymes to distinguish a recombinant product from a nonrecombinant one, and no compelling reason for any given gene to really 'care' whether it has ended up in one configuration or the other.

There is, of course, a gene that actively invokes DSBs, and a whole host of reasons for its persistence, since it has a hugely complex broader phenotype, for something that just snips chromosomes then sits back. But I don't think the rest of the machinery of eukaryotic sex arose *because of* those advantageous distant consequences.

Reply

Replies

1.

Laurence A. Moran Friday, July 20, 2012 12:07:00 PM

I think that the explanation is more local - advantages from diploidy, or a nutritional gain for both partners.

That doesn't work because sex arose in haploid organisms where the "donor" may not gain any advantage and may even be dead.

2.

Allan Miller Friday, July 20, 2012 2:35:00 PM

I think this is where immersion in the worlds of bacterial 'sex', and the norms of modern multicellular sexual reproduction, can cloud the issue. Bacterial conjugation is only analogous to our sex, and neither is a good model for early

eukaryote unions.

Eukaryotic sex at its heart is not a matter of donation and receipt, but of merger. It arose in haploid organisms, most certainly, but the immediate result of a merger of two haploids is a diploid. Sex arose in single-celled organisms, and one cannot really envisage a preceding period during which some of the population became smaller and some larger before syngamy was initiated.

So the primordial state was almost certainly isogamous, symmetric. The genetic and the cytoplasmic contribution of the partners was exactly equal, and despite all subsequent complexification of the process, the *genetic* component remains so. Which I think is a key factor in its ongoing stability.

Reply

6.

Rosie Redfield Friday, July 20, 2012 1:51:00 PM

Larry, are you referring to meiotic sexual reproduction in eukaryotes? Processes that cause genetic exchange in bacteria (including the one with dead 'donors') are not ancestral to that kind of 'sex'.

Reply

Replies

1.

Laurence A. Moran Friday, July 20, 2012 2:30:00 PM

Larry, are you referring to meiotic sexual reproduction in eukaryotes?

No, of course not. Otherwise I wouldn't have said what I said.

Homologous recombination arose long before eukaryotes, not meiosis.

2.

Allan Miller Friday, July 20, 2012 4:48:00 PM

Homologous recombination arose long before eukaryotes, not meiosis.

What relates the homologous recombination of bacteria to that of eukaryotes - beside the mechanistic fact that they both activate repair pathways? They are very different processes, quite possibly performing very different functions, and I think it confuses matters to try and shoehorn them into the same explanatory framework - or to assume there is some kind of historic continuity between the bacterial process and the eukaryotic one, either mechanistically or functionally.

Still, my point on diploidy/nutrition was specifically in relation to a 'meiotic' system,

not any bacterial one. Before you can have eukaryote-syle homologous recombination, you need syngamy and division. And it was for *those* which I suggested diploidy and nutrition as potential reasons (the syngamy part, at least).

3.

AnonymousFriday, July 20, 2012 6:03:00 PM

The key proteins that initiate recombination, RecA in bacteria and Rad51 in eukaryotes are homologous. In the case of recombination there is a definitively established continuity of processes, both mechanistically and functionally.

4.

Allan Miller Saturday, July 21, 2012 4:31:00 AM

RecA and RAD51 are REPAIR enzymes. Naturally enough, they are involved in recombinational processes as well, since these break chromosomes.

But continuity of the kind of recombination under discussion - that involving 'foreign' chromosomes from different organisms recombining - is not demonstrated by homology of proteins involved in some detail of the process. Of course DNA management enzymes are going to be heavily involved. But this is a process, and I don't see where your asserted continuity of *process* resides.

Whenever you break a chromosome, in prokaryote or eukaryote, you invoke a repair pathway, and it is as likely to be homologous as not. But there is a fundamentally different supervening process at work, of which Rad51 homologues form a common 'subroutine'.

5.

AnonymousSaturday, July 21, 2012 9:15:00 AM

The activity of both RecA and RAD51 are to bind single stranded DNA, search for a complementary sequence region in double stranded DNA, then exchange one of the dsDNA strands for the sequence similar ssDNA strand. Neither of these proteins make any changes to any covalent bonds in DNA. The enzymes only recognize the capacity for DNA strands to base pair without regard to the possible 'foreign' source of any of the strands. The current thinking in the field is actually that the most important function of recombination is the restart of stalled DNA replication forks, which explains the essentially universal prevalence of recombination.

With this underlying biochemical activity in place it doesn't take much tweaking to also enable repair of both single and double stranded breaks in DNA using recombination, if a suitable repair template is available (typically the sister chromatid in G2), and we find these processess also to be universal.

With those processes in place, it doesn't take much tweaking to enable

programmed dsDNA breaks to initiate homologous pairing of homologous chromosomes in diploid cells. These programmed breaks are caused by SPO11, with nearly universal conservation in eukaryotes. It is at this tertiary functional level that there appears to be divergence between bacteria and eukaryotes. Interestingly, the primary necessity for recombination in eukaryotic meiosis is to align the parental homologs so the first meiotic division can evenly partition chromosomes to daughter cells. The layperson view of meiotic recombination as the shuffling around of genes is nearly at the level of a happy accident in terms of mechanistic importance.

6.

Allan Miller Saturday, July 21, 2012 10:04:00 AM

With those processes in place, it doesn't take much tweaking to enable programmed dsDNA breaks to initiate homologous pairing of homologous chromosomes in diploid cells.

Well yes, that is close to what I've been saying. Conservation of DNA repair pathways is unsurprising, and meiotic recombination at the DNA level is distinguished not by a brand new toolkit, but by the stirring into life of that toolkit by Spo11-induced DSBs. But it is also distinguished by a whole panoply of mechanisms that get these chromosomes into close approach in the first place. I can't see any plausible continuity between the prokaryotic mechanism of providing substrates for RecA and the eukaryotic one for RAD51.

The layperson view of meiotic recombination as the shuffling around of genes is nearly at the level of a happy accident in terms of mechanistic importance.

Nonetheless, 'gene-shuffling' is a prevalent view, even among non-laypersons, and when people talk of bacteria having sex because they perform some kind of recombination, I think this is apt to confuse, hence my preference to avoid the confusion of sex with recombination. The homology of some of the proteins involved does not necessarily point to a homology of function.

Recombination is not, I think, the reason there is a syngamy/meiosis cycle. However, a syngamy/meiosis cycle does provide a very close approach for near-homologues, which allows pre-existing recombination pathways to be invoked.

Sex, per se, was a brand new invention of the eukaryotes, albeit one co-opting many prior pathways.

7.

AnonymousSaturday, July 21, 2012 12:00:00 PM

AM: *Recombination is not, I think, the reason there is a syngamy/meiosis cycle. However, a syngamy/meiosis cycle does provide a very close approach for near-homologues, which allows pre-existing recombination pathways to be invoked.*

Actually, this is exactly the reverse of the current thinking in the field. It is the homology search of recombination that provides the mechanism for the close approach of homologs/near-homologs and not that the close approach of homologs provides an opportunity for recombination. This is a relatively recent change in thinking brought about largely by studies of meiosis in mice with gene knockouts/hypomorphic alleles of proteins involved in recombination (1). For example, absent SPO11, there is no chromosome synapsis and no formation of bivalents. These types of experiments make clear that in meiosis, recombination precedes and is required for synapsis.

(1) Recombinational DNA double-strand breaks in mice precede synapsis Shantha K. Mahadevaiah et al., Nature Genetics 27, 271 – 276 (2001)

8.

Allan Miller Saturday, July 21, 2012 9:15:00 PM

Recombination is undoubtedly intimately involved in modern meiosis. But you don't get the chromosomes anywhere near each other without syngamy, and I don't think the role of syngamy is to provide raw materials for meiosis, with or without recombination. Something of a quite extended nature happens before meiosis ever comes into play, and I think it's worth looking at this for the root explanation of the cycle.

There is a diploid phase, which may involve many rounds of mitosis - an opportunity to amplify both haploid genomes in a double-organism with several potential advantages over the go-it-alone route.

Ultimately, there has to be a reductive step - this, essentially, reconstitutes the original haploid organisms. While modern meiosis may be crippled by inability to use crossovers to stabilise bivalents on the metaphase plate, I don't think this forces that constrain on all versions of the process. If you need the complexities of recombination before you can successfully reduce, the cycle will never get going.

Merging two haploid organisms fast-forwards the cell cycle along the growth phase. To the machinery of mitosis, the syngamous diploid may look just like a post-S-phase cell, albeit without centromere attachment of these pseudo-sisters. Division is initiated, using pre-existing (presumably non-recombinational) mechanisms to detect and align near-homologues and reliably haul them apart - a proto-meiosis ll. This may not need the close approach of synapsis - particularly if the organism had only 1 chromosome in the haploid set. Only later does recombination come into the frame, as part of what is now Meiosis l.

9.

AnonymousSunday, July 22, 2012 12:03:00 PM

I'm not sure I understand what you're saying. Modern meiosis does use crossovers to stabilize bivalents on the metaphase plate. The process is quite tightly regulated; see particularly the work from Neil Hunter's lab for a modern treatment of the

problem in cerevisiae.

The crux of any cell division problem, either mitosis or meiosis or whatever, is the correct partitioning of chromosomes to daughter cells in multi-chromosome organisms. How, mechanistically, can the cell identify which chromosomes are a match for each other? Currently there are two mechanisms: 1) keep the matched chromosomes physically attached to each other at all times, for example through cohesin attachment of sister chromatids, 2) somehow "read" chromosome sequence information to identify matches; this is what the core recombination machinery (RecA/Rad51) does. Since recombination is ancient, precedes sexual reproduction of eukaryotes and can do the job, there is no need to postulate "*pre-existing (presumably non-recombinational) mechanisms to detect and align near-homologues and reliably haul them apart*".

10.

Allan Miller Sunday, July 22, 2012 2:56:00 PM

I guess my angle would be that meiosis - and its recombinational element - are hugely complex, multi-protein affairs. The explanation of their origin needs to account for plausible stepwise accumulation of the complexities. However, even simple versions of a recombinational role in early meiosis requires more than one protein to successfully do a brand new job. And, IMHO, it needs to happen in a single generation.

If we postulate a syngamy that the cell was already 'preadapted' to be responsive to, and lead ultimately to successful reduction, we can certainly include the fact that recombination will be automatically invoked *if* there is close approach of homologues *and* there are DSBs. Shove chromosomes next to each other and they do not automatically recombine. They do so only if something nicks them.

From an ancestral population of free-living haploids, some of them instigate syngamy. As far as I can see, if DSB + recombination is essential for severance of the union, then they are stuck like that - perpetual diploids. Which may not be a bad thing, but is not the cyclic system. (It may be a bad thing if mitosis cannot yet cope with multiple chromosomes either).

So you need reduction. A cytoskeletal system needs to be invoked to haul chromosomes apart - but I would query the insistence that this process cannot take place without recombination. Sure, it cannot *now* ... usually.

You are suggesting that the only - or perhaps, the likeliest - way to partition chromosomes not physically joined is to perform recombinational sequence search. Is it the case - even now - that homologues will not pair up unless one of them has at least one DSB? Genuine question; I don't know. This seems a particularly error-prone method for pairing homologues. They are a pair if a few hundred bases are homologous (though, as non-sisters, they aren't certain to be *that* homologous in that region)? I may be stabbing wildly, but I think there are other pair-recognition mechanisms in operation, even today.

But a third option I suggested, you missed out: it is entirely conceivable that, initially, there was only one chromosome per haploid partner. No sequence recognition is then necessary, nor physical joining. Opposite spindles attach to a chromosome each, and pull.

This separation mechanism might well benefit from crossover stabilisation, and would struggle with multiple chromosomes, but start clumsy and get refined would be the likely evolutionary path.

I do find it a bit of a swallow that, the very first time a haploid-diploid-haploid cycle was undergone, there were already multiple chromosomes which, following successful syngamy and a viable diploid phase, a close enough synapsis, DSBs and recombinational (re)pair-recognition all just happened to be up to this brand new job of pairing and separating not-quite-homologues.

11.

AnonymousSunday, July 22, 2012 4:31:00 PM

Is it the case - even now - that homologues will not pair up unless one of them has at least one DSB?
If you mean synapse to form a bivalent, then yes, at least one recombination-initiating event is required (SPO11 makes DSBs, but other possibilities are conceivable such as spontaneous oxidative lesions resulting in chromosome nicks and gaps), and further at least one crossover is required.

This seems a particularly error-prone method for pairing homologues.
Perhaps so.

They are a pair if a few hundred bases are homologous (though, as non-sisters, they aren't certain to be that homologous in that region)?
The pairing seems to be an interative multi-stage process. The initial sequence sampling by RAD51 only looks at maybe 20 bases at a time. When found, that initiates polymerization of a RAD51 filament down the length of the chromosomes. There is a proofing step: the mismatch repair system is invoked to check the presynapsed regions for suitable sequence complementarity. If the complementarity is less than about 98%, the mismatch repair system dismantles the recombination structure and the cell can try again. Note that the mismatch repair system, similar to the recombination machinery, is also ancient with essentially complete protein and mechanistic conservation from E. coli to humans and everything in between.

It is entirely conceivable that, initially, there was only one chromosome per haploid partner.
To me this seems plausible. It is supported by the observation that recombination is NOT absolutely required for at least low-frequency correct segregation of parental homologs in S. pombe. This yeast has only three chromosomes, and presumably manages to partition successfully at least some of the time by sheer stochastic process.

I may be stabbing wildly, but I think there are other pair-recognition mechanisms in operation, even today.
I don't know of any, and it would seem unnecessary to reinvent the wheel at it were given that recombination was already in place as such a mechanism.

I do find it a bit of a swallow that, the very first time a haploid-diploid-haploid cycle was undergone, there were already multiple chromosomes which, following successful syngamy and a viable diploid phase, a close enough synapsis, DSBs and recombinational (re)pair-recognition all just happened to be up to this brand new job of pairing and separating not-quite-homologues.
Note again that recombination causes synapsis, not the other way around. If I were to guess, it would be the initial conversion to diploidy resulted from simple cytokinesis failure in mitosis rather than cell-to-cell fusion. One could envisage a haploid proto-cell with a small number of chromosomes that periodically undergoes mitotic non-disjunction to become pseudodiploid. A reciprocal mitotic failure, cell division without preceding DNA replication, could restore the cell to haploid status. With the machinery of homologous recombination and mismatch repair already in place, it wouldn't take much tweaking for spontaneous DNA damage to be exploited and then enzymatically amplified to initiate recombination and greatly increase the fidelity of the process, thereby enabling an increase in chromosome number. Cell-to-cell fusion ("mating") would be pretty easy to add-on later once the proto-cell got good at reductive division.

12.

Allan Miller Monday, July 23, 2012 4:36:00 AM

If I were to guess, it would be the initial conversion to diploidy resulted from simple cytokinesis failure in mitosis rather than cell-to-cell fusion

Possibly, but the diploid so formed is of a very different character – homozygous at every locus. – than that resulting from syngamy. The syngamous diploid has the potential for immediate advantage – 'cheap' increase in size, masking deleterious loci etc. This introduces a very different dynamic: a mutually beneficial union between organisms. And it has access to a pre-existing mechanism for separation, without invoking rather complex recombinational pairing via 'controlled' DSBs: *mitosis*. If one postulates a single chromosome, there is no need for sequence recognition at that early stage.

But take a cell with a rather incompetent mitosis and develop a second process to crowbar the diploid apart, the advantage being that you end up with the same cells as those with competent mitosis? … I find it doubtful. I think it most likely that the conserved processes continued to do their 'original' job in early syngametes, recombinational repair, being co-opted into the reduction phase at a later date, possibly when multiple chromosomes demanded a pairing system in the absence of centromeric joins, or genetic conflict demanded a mechanism for confounding a 'self/non-self' distinction.

Reply

7.

Rosie Redfield Friday, July 20, 2012 6:01:00 PM

Larry, this is why we should avoid use of the word 'sex' in discussions of the evolution of recombination processes. This word has many possible meanings, and the truth of your statement depends on which meaning is applied.

Your response implies that the onus was on the reader (me) to choose the interpretation of 'sex' that made the statement correct. But really the onus should be on the source (you) to make sure that your statement is not ambiguous.

Reply

Replies

1.

Laurence A. Moran Friday, July 20, 2012 10:30:00 PM

The main point of my post (above) and our discussion in Ottawa was that we are using different definitions of " sex." I apologize for not making that clear.

Your blog posting assumed one definition of " sex" but I don't think it's the most common one.

Reply

8.

Sergio Muñoz Saturday, July 21, 2012 1:51:00 AM

I recommend each of you post your formal definitions of sex.

I think the word sex cannot be applied to any mechanism that may accidentally results in the exchange of alleles, even if there is an external source of genetic material. Sex should refer to the eukaryotic process of reciprocal genetic recombination resulting from the alternation of meiosis and syngamy (cell fusion). Sex is unique to eukaryotes, it evolved prior to their cenancestor and it is usually linked to reproduction, but there are exceptions like conjugation in ciliates. It is such a complex process that it has evolved just once in the history of life; several eukaryotic lineages appear to have lost it. Mechanisms for DNA transfer and exchange among prokaryotes ("bacterial sex") has nothing to do with (sexual) reproduction as it usually happens in eukaryotes.
Other important distinction as it has already been mentioned is that genetic exchange/recombination mechanisms in bacteria are unidirectional and not reciprocal in contrast to the selective advantageous evolved process of sex in eukaryotes.

My personal opinion is that transformation evolved as a means to take DNA as a source of nutrients, conjugation is a process to spread selfish genetic elements where the cell is manipulated by the gene-level selected plasmid or virus-like element, and transduction is just the accidental outcome of the bacteriophage's life cycle.

The molecular cell machinery for recombination in prokaryotes is probably homologous to that of eukaryotes, or at least many components of it are, but they also probably evolved for DNA repair and not for the "purpose" that sex has in eukaryotes. It is difficult to know what was the source of the homologous genetic material used by the original DNA repair machinery, it could have been an external source or an internal one (e.g. multiple bacterial chromosomes in the same cell).

It may be possible that several of these mechanisms in prokaryotes have been recruited for its beneficial genetic consequences by increasing variation and avoiding Muller's ratchet. In this sense they could be playing the same role that in eukaryotes, but they are completely different,convergent and non-homologous processes that evolved initially for different reasons.

This putative, but plausible, current role of DNA transfer mechanisms in prokaryotes must be tested.

Reply

Replies

1.

Allan Miller Saturday, July 21, 2012 4:46:00 AM

Sex should refer to the eukaryotic process of reciprocal genetic recombination resulting from the alternation of meiosis and syngamy (cell fusion)

I agree! If one insists that that sex = recombination, or is persuaded by pictures of bacterial pili to think of gendered sex in multicellulars, I think one is at risk of confusing very different processes. Sex = syngamy/reduction, which may or may not include a recombinational phase. Bacteria are mostly infecting each other (though not necessarily detrimentally).

People have been looking for a workable reason for (eukaryotic) sex as a vehicle for recombination and its distant benefits for years, and I think the reason it has not been conclusively found is that it is not there. Recombination plays a role within meiosis (eg bivalent stabilisation, and potential chromosome-killer silencing), and has massive multi-level consequences for the clade we are in, but is not the reason there is meiosis.

It is difficult to know what was the source of the homologous genetic material used by the original DNA repair machinery

Post-replication pre-fission material, probably.

2.

Allan Miller Saturday, July 21, 2012 5:10:00 AM

Sex should refer to the eukaryotic process of reciprocal genetic recombination resulting from the alternation of meiosis and syngamy (cell fusion)

Actually ... I disagree! But only because of the retention of emphasis upon recombination. It happens, but it is almost incidental. Sex is the cycle itself, not something that happens within it. Recombination is almost an afterthought in the life cycle, which largely consists of the often-bloated diploid formed from syngamy.

Given a cycle of haploid merger and diploid separation, recombination of some kind is unavoidable if there is more than one chromosome in the haploid set. Chromosomes are not labelled 'his 'n' hers', and nothing cares which way they segregate. 50% of the time, parental haploid sets will separate in the next generation, if n=2. A gene cannot tell whether it has remained linked to its previous organism-fellows or not, and has no reason to care, if both results are equally viable.

This is mechanistically very different from the DSB-mediated process, which greatly increases the permutations, but with similar effect and constraint. Recombination *happens* to increase variation, speed up evolution, purge detrimental mutations and combine beneficial ones [etc]... rather than being there *because* it does.

Reply

9.

LisaSunday, July 22, 2012 1:30:00 PM

Great question and bacteria is homo sexual and they have sex internally..i think so.Sexuality

Reply

10.

Rosie Redfield Sunday, July 22, 2012 4:10:00 PM

@Sergio, @Allan,

You're both making the mistake of thinking that 'sex' has a specific meaning, with our problem being to decide what that meaning is or should be. Instead we need to face the reality that word meanings are genuinely and inevitably fluid and user-dependent, and that trying to impose a single definition is a waste of time.

This becomes especially evident when we mistakenly try to argue about whether something is a valid instance of a category we're interested in (e.g. Is conjugation an instance of sex? Is this group of organisms really a species? Is a virus an instance of 'life'? Is what I feel really love?). That's because, although the category words work fine in relaxed usage, the nature of language means that they don't have precise meanings unless all users agree to one.

The solution isn't to enforce a definition (of 'sex;' or anything else), telling people what the word should mean, but to just take pains to be clear about what we do mean. It's usually best to avoid the problem word entirely. That's why my research question asks whether bacteria have processes that evolved because of selection for the ability to create recombinant genotypes, and I use 'Do bacteria have sex?' only as a teaser that's immediately followed by the clarification.

Reply

11.

Allan Miller Monday, July 23, 2012 9:15:00 AM

Rosie,

I agree that this may smack of arbitrary 'definology', much like the word games played by creationists. But given that the OP asks the direct question, the answer 'if you define it thus' does not fully satisfy.
If there is a reaon for choosing a word for a phenomenon, there is legitimate cause for objecting to that usage.

Words unavoidably trigger associations, particularly words that are also in common usage. Historically, the biological usage of 'sex' covered something much like the process noted amongst ourselves and our domesticated associates whose essential character is biparental inheritance. Drilling down, we noted both that there are variation-generating/ reductive steps, and that prokaryotes performed something which had analogies to the multicellular eukaryotic process at both a high (conjugation) and a low (recombination) level. And at a low level, the functional implementation of recombination involves significant homology, not just analogy. So at some point, 'sex' shifted to mean recombination. No-one is going to shift their usage on my account, and I realise that people are perfectly capable of not being misled by word usage, there is nonetheless an element of question-begging when sex is equated directly with recombination - as in:

That's why my research question asks whether bacteria have processes that evolved because of selection for the ability to create recombinant genotypes,

They may well do. But this does not mean that the eukaryotic syngamy/reduction cycle evolved because of selection for recombinant genotypes. Per my discussion with 'Anonymous' above, eukaryotic recombination could be a byproduct of reduction (he/she favours a Stage 1 requirement for pair recognition, I a subsequent amendment of a pre-existing syngamy/reduction cycle).

So, it's not so much a question of telling people what 'sex' should mean, but arguing for a separation of process - syngamy/reduction from recombination, and of bacterial recombinant processes from eukaryotic ones. Even if there is homology of sequence, there need not be homology of 'cause'. Syngamy, eukaryotic sex's most distinctive feature, seems to get all-but-forgotten in 'mystery of sex' treatments in favour of a couple dozen theories based upon recombination.

Reply

12.

Rosie Redfield Tuesday, July 24, 2012 4:17:00 PM

Wait, 'recombination' has different meanings too! Do you mean the production of recombinant genotypes or the physical breaking and rejoining of DNA molecules into different combinations?

And, if recombination (in the former sense) in eukaryotes is a byproduct of reductive division, why would eukaryotes need regular reductive divisions in the first place? This takes us back to the big question - why has meiotic sexual reproduction been so successful in eukaryotes?

Reply

13.

Joachim D. Wednesday, July 25, 2012 1:31:00 PM

Gynogenetic, hybridogenetic, and androgenetic organisms reproduce sexually and yet they do not have meiotic recombination. The haploid genome of one of the sexual partners gets lost in the life cycle. In gynogenesis the male genome gets lost from the zygote and in androgenesis the females genome is thrown out. In hybridogenesis the male genome gets into the soma but not into the germ-line. So here we have examples of organisms that are sexual but have no meiotic recombination.

On the other hand, bacterial recombination is an example of recombination without sexual fusion, meiosis and all that. To call bacterial gene-swapping sex is IMHO as confusiong as calling hybridogens asexual, though it's sometimes a convenient shorthand - that is, if it can be assumed that it will not lead to confusion of the other party.

Reply

14.

Allan Miller Wednesday, July 25, 2012 8:28:00 PM

Rosie: *Wait, 'recombination' has different meanings too!*

Fair comment. There is less of an issue here, though, due to greater consistency among the phenomena, and the lack of baggage associated with the word.

Do you mean the production of recombinant genotypes or the physical breaking and rejoining of DNA molecules into different combinations?

Ummmm ... yeah! Some processes are only one of these, some both. But ultimately, they all share the character of 'mixing genes up'. Meiosis incorporates both, with two different mechanisms – DSB-mediated reciprocal exchange, and stochastic segregation of multiple chromosomes.

But sex - when a bacterium picks up a bit of environmental DNA from a burst cell, that's sex? Or gets a bit that got lodged in the capsid of a virus? Or even one donates a selfish genetic element via conjugation? It's madness, I tell ya! :0)

And, if recombination (in the former sense) in eukaryotes is a byproduct of reductive division, why would eukaryotes need regular reductive divisions in the first place?

My own ten cents, taking a 'cycle-first' view, is that reduction may have been, initially, unavoidable. Mitotic fission is triggered by cell cycle growth, subsequent to the S phase. If you merge two haploids in one, you have a bigger cell and two chromosomes. Persuading mitosis *not* to kick in may have been the first challenge. It is also possible that such diploids could not themselves perform full mitosis, if primitive mitosis was incapable of dealing with multiple chromosomes. Either way, haploidy is simply the organisms returning to their 'native' state. The main 'job' of the diploid is to house the haploids: a binary organism. Subsequent enhancements may include polyploid mitosis, recombinational meiosis, increasing prominence for the diploid phase and diminished significance of the haploid, until there is a perceptual reversal of the original relationship.

This takes us back to the big question - why has meiotic sexual reproduction been so successful in eukaryotes?

Syngamy and recombination! It's clear that recombination is a massively important consequence of sex. But so is syngamy. The diploid is a generally more satisfactory package than a 'bare' haploid, for several reasons. But the best way out of a diploid organism is riding on a haploid gamete. If you remain in the sexual milieu, you can tune both phases much more rapidly.

There may be a period, before recombination, when cyclic diploidy does little or no better than permanent diploidy. But once 'full sex' gets going, the sexual world has standing variation, and a faster rate of evolution and hence of cladogenesis. Asexual revertants typically flip into 'slow time', compete less effectively and diverge less, so there aren't so many of 'em.

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